OBSERVATIONS ON MATING, OVIPOSITION, AND FOOD HABITS OF CERTAIN SHORE FLIES (DIPTERA: EPHYDRIDAE)[1]

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ABSTRACT

Some observations on mating and oviposition behavior in some common midwestern species of ephydrids are described. The mounting phase of mating in *Ochthera mantis* (DeGeer) appears to consist of simple, rapid jumping and grasping movements by the male. The male taps the abdomen of the female with his hind tarsi during copulation. Copulation is similar in *Parydra quadrituberculata* Loew. During seven days of captivity, two females of the latter species deposited 119 separate egg masses, each containing from two to eleven eggs. Oviposition sites such as small rocks and twigs extensively encrusted with egg masses of this species were commonly found in field habitats.

Shelter-seeking behavior was also observed. Adults of *Ochthera mantis* (DeGeer), *Parydra quadrituberculata* Loew, *Scatella stagnalis* Fallén, and *S. quadrinotata* Cresson obtained shelter by clustering in numbers on vegetation and other high objects during heavy rainfall and darkness.

The hypothesis that diatoms constitute a potential, abundant, and available food source for shore flies was also tested. The gut contents of specimens representing 30 ephydrid species were surveyed by dissection and by nitric acid digestion of masses of whole flies. The presence of diatom frustules in these guts was interpreted to support this hypothesis.

INTRODUCTION

The majority of the described species of shore flies, or Ephydridae, are semi-aquatic as adults and aquatic in the immature instars. Many species occur only in maritime (or inland saline) habitats and many others are limited to fresh-water habitats; others are found in both types of habitats. Until relatively recently, the habits of Ephydridae had not been studied to any extent. The few recent studies of ephydrid habits have concentrated mainly on the halobiontic and thermobiontic members of the subfamily Ephydrinae and on the leafmining notiphiline genus *Hydrellia*. Several observations and data on mating, oviposition, and food habits in species of *Hydrellia* were presented by Deonier (1971). The work by Dahl (1959) in Scandinavia is the only extensive ecological treatment of this family as a whole.

In the Nearctic Region, Aldrich (1912) conducted one of the first natural history studies on species of *Ephydra* in the principal saline and alkaline lakes of the Great Basin. Aldrich found adults of *Ephydra cinerea* Jones (as *E. gracilis* Packard) and *Ephydra hians* Say to be very abundant on these lakes, despite the extreme salinities (to 32 percent) of the water in some of the larval habitats. Indeed, for one locality on Great Salt Lake, Aldrich (1912, p. 83) stated that, "The minimum estimate would give about 370,000,000 flies to the mile of beach". Considering these enormous populations and the biomass represented by these flies, the very scant attention given to their food and other habits is surprising. Aldrich, in this same study, could only surmise that the flies of *E. cinerea* were feeding on *Nostoc* algae. Another writer, Jones (1906), could only conjecture that *Ephydra millbrae* Jones, a California species, might also be algophagous. Neither author presented any data on the mating habits of these ephydrine species.

Much more detailed data on the food and other habits of both larvae and adults of a related Atlantic Coast species, *Ephydra subopaca* Loew, was presented by Ping (1921). Brauns (1939) studied the feeding action and food of adults of the Palaearctic ephydrine, *Scatella subguttata* Meigen. Tuxen (1944) studied

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the habits, especially the feeding habits, of larvae and adults of *Scatella thermarum* Collin in hot springs in Iceland. Nemenz (1960) included observations on the food habits of *Ephydra cinerea* in a physiological study of the species. Recently Brock and Brock (1968) and Brock *et al.* (1969) studied oviposition and food habits in *Ephydra bruesi* Cresson and in *Paracoenia turbida* Curran, two thermobiontic ephydrines occurring in hot springs in Yellowstone National Park.

The objectives of the present study were two-fold: to record observations on mating and oviposition behavior in some common midwestern ephydrid species, and to survey the extent of algophagy (algae feeding) in an inland freshwater ephydrid fauna.

MATERIALS AND METHODS

Instances of mating, oviposition, shelter-seeking, and feeding behavior were observed in *Ochthera mantis* (DeGeer), *Parydra quadrituberculata* Loew, *Scatella quadrinotata* Cresson, and *Scatella stagnalis* Fallén. In addition, one instance of oviposition and one of shelter-seeking behavior were observed in *Discocerina lacteipennis* Loew. Unless otherwise specified, these observations were made in the field during daylight in clear weather and while at a distance of about one foot from the flies. Some laboratory observations were made on adults of *Ochthera mantis* and *Parydra quadrituberculata* kept at room temperatures in small field-simulated habitats contained within screen-covered five-gallon aquaria. These habitats were made by carefully transferring a relatively undisturbed section of the substrate (including vegetation growing on it) from the natural habitat to the aquaria. Distilled water was added to these habitat extracts when needed to maintain the original amount of water, but no nutrients were added.

In this study, the term observation means the witnessing of a distinct occurrence of a particular behavior pattern from its initiation to its termination. The length of each observed instance of a behavior pattern was necessarily demarcated by the exhibition of some other behavior pattern, e.g., feeding—mating—feeding. Flies observed in the field were captured and preserved at the end of each observation. In the observations of feeding, the flies were captured after they had started to ingest the food. Those adult flies observed within the laboratory were allowed to live on and preserved after they had died. Voucher specimens preserved during this study are located in the Iowa State Insect Collection and in my own collection.

The localities at which behavioral observations for each species were made are as follows:

Ochthera mantis

INDIANA: 0.4 mile south of Bath, Franklin County. IOWA: Izaak Walton Reserve near Ames; Ledges State Park, Boone County; 4 miles east of Gilbert, Story County. NORTH CAROLINA: Highlands Biological Station, Macon County. OHIO: Acton Lake, Preble County; Fisher Pond and Western Pond, Oxford. VIRGINIA: Johns Creek, 1 mile east of Maggie, Craig County.

Parydra quadrituberculata

IOWA: Izaak Walton Reserve near Ames; Clear Creek in Ames; Skunk River in Ames; north bank of Des Moines River near Ledges State Park, Boone County; 4 miles east of Gilbert, Story County. NORTH CAROLINA: Highlands, Macon County. OHIO: Acton Lake, Preble County; Little Four Mile Creek, Hueston Woods State Park, Preble County; Fisher Pond and Western Pond, Oxford. VIRGINIA: New River, 0.6 mile south of Eggleston, Giles County; Sinking Creek, 0.25 mile east of Newport, Giles County.

Scatella quadrinotata

IOWA: Pease Creek, Ledges State Park, Boone County; White Pine Hollow State Park, Dubuque County; 3.5 miles west of Boone, Boone County.

Scatella stagnalis

IOWA: Clear Creek in Ames; Botany green house, Iowa State University, Ames; Ledges State Park, Boone County; North bank of Des Moines River at Fraser. OHIO:

Fisher Pond, Oxford. VIRGINIA: Spruce Run, 4.5 miles south of Newport, Giles County.

Discocerina lacteipennis

IOWA: Mississippi River, 4 miles south of Oakville, Louisa County; North bank of Des Moines River, Ledges State Park, Boone County.

The survey of food habits in inland ephydrids was done by two methods. In one method, the gut was removed and its contents placed in a temporary tap-water mount to examine for the presence of diatoms and of other algae. After this initial examination, a sample from the temporary mount was placed in a drop of 20 percent hydrogen peroxide on a cover slip, heated slowly for about ten minutes to clear any diatoms present, and then permanently mounted in Hyrax medium. The remainder of each temporary mount of the gut contents was allowed to dry between two cover slips for storage as additional voucher specimens. In the other method, whole shore flies were washed in a detergent solution and then digested in a hot solution of 20 percent nitric acid. After digestion of the flies was complete, the preparation was first allowed to cool and then the acid was decanted from it. Samples of the undigested gut contents (diatom frustules and some sand particles) were permanently mounted in Hyrax® medium.

BIOLOGICAL OBSERVATIONS

Mating and Oviposition

Mating in *Ochthera mantis* was observed in the field on three occasions. In these observations, the male mounted the female from behind by what appeared to be rapid jumping and grasping movements. (In one instance, the female turned and struck at the male with her fore legs after he had jumped at her.) In laboratory observations of five isolated pairs, male and female spread and flexed their fore legs several times during the approach of the male and before mounting was attempted. However, since this fore-leg spreading has been observed on numerous occasions to be elicited by the approach of members of the same sex and even of other species (and orders), it may be a threat or recognition display that is not actually integrated into the courtship.

In the field observations, after the male had mounted and grasped the humeral plates of the extended wings of the female with his fore tarsi, he began to tap the sides of her abdomen rapidly with his hind tarsi. During the subsequent insemination phase, the male moved his abdomen posteroventrad, assuming a nearly vertical attitude in relation to the female. He then began a bouncing movement to which the female may have contributed. Duration of copulation was five minutes in one case.

In the first observation of mating in *Ochthera mantis*, two other males attempted to mate with the recently inseminated female, but she rejected them. Immediately after this occurrence (and thirty minutes after copulation), the female oviposited twice in the mud at the base of a grass stem. This female was then captured and retained in a field-simulated habitat within an aquarium where she oviposited about every 2.5 minutes at least ten times, each time placing a single black, elongate-ellipsoidal egg in or on dead, water-soaked grass stems.

Parydra quadrituberculata showed no conspicuous courting, or posturing, behavior in its mating, as witnessed in at least twenty observations during two summers. However, the other phases of mating were very similar to those in *Ochthera mantis* except that no noticeable rapid palpation of the female by the male took place. However, oviposition as observed in *P. quadrituberculata* was distinctly different from that in *O. mantis*. During seven days in captivity, two females of the former species deposited 119 separate egg masses on the glass of an aquarium. Each egg mass contained from two to eleven white, elongate-ellipsoidal eggs. Each egg mass was covered with a light-green layer of feces

containing diatom frustules, sand grains, and pigments. Most of the eggs hatched, and five of the larvae were reared to adults. Several larvae in each instar were killed and preserved, as were several pupae, but several other larvae died in the first and second larval instars and were subsequently lost in the mud. In at least eleven field observations, females oviposited on rocks or fallen twigs, or other dry surfaces projecting above the flat muddy ground. Certain of these oviposition sites were examined in the same locality repeatedly during several trips. The number of egg masses increased through the week to the point of the extensive encrustation shown in Figure 1. This seemed to be explained partially

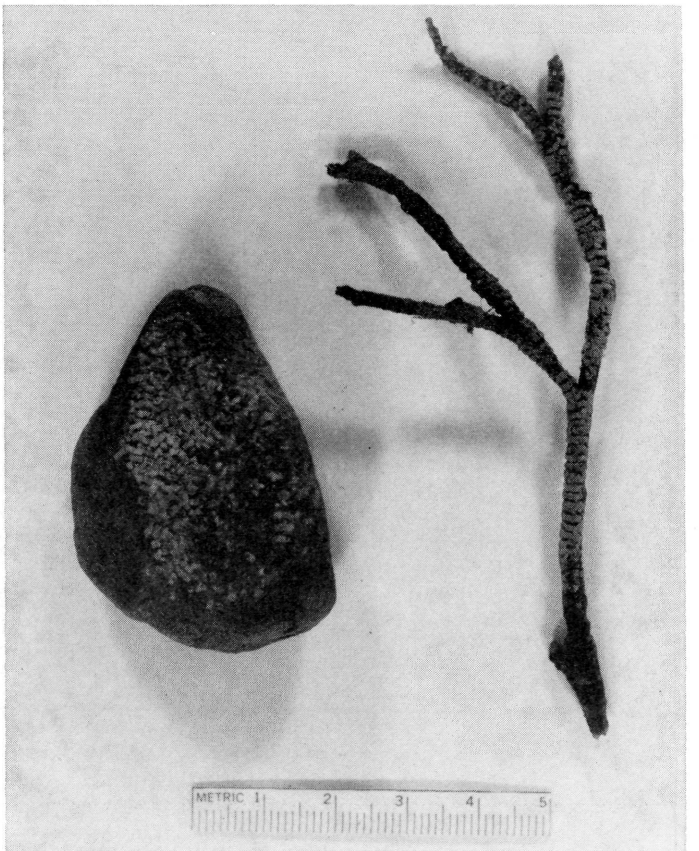

FIGURE 1. Egg masses of *Parydra quadrituberculata*. The rock and twig are covered by several hundred egg masses, probably laid by several females. The effect of shape of oviposition substrate upon egg-mass arrangement is apparent in comparing rock and twig.

by the small number of desirable, readily available oviposition sites projecting above the flat muddy ground, and the use of these by several females. The larvae that eclosed from these egg masses were determined to be *Parydra quadrituberculata*.

The six field observations of courtship and copulation in *Scatella stagnalis* reported here parallel closely the process described for the species in Scandinavia by Dahl (1959). In my observations the male approached the female from the front, using a slow sidewise walk until he had reached a point about three centimeters from her, following which he walked very slowly directly toward her. A

few millimeters from her, he stopped and "scissored" his wings three times. The male then moved forward so that his antennae seemed to touch those of the female, after which he walked alongside the female. When she partially spread her wings, he mounted her abdomen. In this process, the male used his fore tarsi to grasp the female's wings near the first costal break. During the ensuing intromission and insemination phase, the male elevated the front of his body, all the while grasping the female's wings. The copulating pair remained mostly stationary with the female only occasionally walking slowly and feeding.

In four observations, the females deposited eggs, usually singly, but at close intervals in mud and in blue-green algae. Oviposition in *Scatella quadrinotata* was observed once; the female deposited eggs singly and occasionally in small masses in algae and moss on a rock exposure near the waterline of a stream.

Unlike the preceding ephydrid species, *Discocerina lacteipennis* seems to prefer moist sand for oviposition. In my one record of oviposition in this species, six females were seen ovipositing during a brief time period in sand within a small area about 50 centimeters from the waterline on a river sand bar. One of these flies selected a small lump of wet sand in which to oviposit. She forced her postabdomen into the substrate, remained stationary briefly, and then rapidly moved her abdomen anteriad and then laterad several times. This action would seem to serve to cover the deposited egg. Only six eggs were located and separated from the sand where the six females oviposited. The eggs were white, elongate-ellipsoidal, and had a small pedicellate process at one end. Only two larvae eclosed; one was preserved and the other one died after two days.

Diel Rhythm and Feeding Activity

The activity rhythms of only a few species of Ephydridae have been investigated. Dahl (1959) recorded observations on the daytime habits and activity rhythms of several species, but he included nothing on their nocturnal habits.

In the present study, the diel rhythm of over 100 individuals of *Parydra quadrituberculata* was observed in the field during two summers. Daytime activity consisted mostly of alternate periods of feeding on littoral mud and of resting on vegetation or other objects near the flat muddy ground surface. A fly, after alighting upon the substrate, would begin to move slowly about, hesitating in various spots to tap the substrate with one or both fore tarsi; it might then protract its proboscis and feed with very rapid, mostly anteroposterior, oscillations of the labella. This searching and feeding activity usually continued for a period of from three to five minutes, followed by an interval in which body cleaning took place. Feeding might then be resumed, or the fly might rest on the vegetation. Large numbers of adults were commonly seen feeding together in one spot so that a small area of mud would appear to be completely covered by them. At one site, two swings of a standard aerial net yielded 300 adults of this species.

Short rain showers did not noticeably alter this daytime activity rhythm, but during longer, heavier rains, the flies did not feed. During such weather, the flies congregated in large numbers on shoreline vegetation. This shelter-seeking behavior during protracted, heavy rainfall was observed on at least six occasions. They also exhibited this behavior at dusk each day. They were found aggregated, facing upward, on grasses, sedges, and other objects projecting above the mud surface. They were not readily disturbed by the light from a flashlight and flew from their perch only when the light was brought very close to them. Instances of this nocturnal shelter-seeking behavior were also observed in *Discocerina lacteipennis*, *Ochthera mantis*, and *Scatella obsoleta*.

Food Habits

The results of observations on the food habits of *Ochthera mantis* made in this study are, in general, similar to those reported on the food habits of various other

species of *Ochthera* by Hobby (1931), Travis (1947), Bohart and Gressitt (1951), and Sturtevant and Wheeler (1954). However, one type of feeding behavior not previously reported was observed in *O. mantis*. In the first observation of this behavior pattern, the fly repeatedly probed the substrate with its proboscis and, after doing so extensively at one point, it excavated with its fore tibial spines a chironomid larva. The predator held the larva between the tibiae and femora of its raptorial fore legs, punctured it with its labella and began consuming it. Soon after this, its feeding was interrupted by the sudden approach of a specimen of *Lispe* sp. (Diptera: Muscidae). Later this same specimen of *O. mantis* captured and fed on a small homopteran nymph. This probing into mud was observed ten times in *O. mantis* and once in *O. lauta* Wheeler (a rare specimen).

The following species were observed to be prey of *Ochthera mantis* in the present study: *Hydrellia griseola* (Fallén), *H. cruralis* Coquillett, *Discocerina obscurella* (Fallén), and one chironomid species (all Diptera), and one delphacid species (Homoptera). Hobby (1931) reported a chloropid as a prey of *Ochthera* in England. Travis (1947) reported *Ochthera canescens* Cresson preying on the larvae of the mosquitoes, *Culex annulirostris* Skuse and *C. quinquefasciatus* Say, and on bloodworms (Chironomidae) in the Solomon Islands and Mariana Islands. On Guadalcanal, Travis found *Ochthera brevitibialis* de Meijere preying on anopheline mosquito larvae and bloodworms. According to Travis, this species of *Ochthera* was sometimes numerous enough to cause reductions in local populations of anopheline mosquitoes. The flight of *Ochthera* was observed to be rapid and close to the water or the ground. Travis indicated that species of *Ochthera* fed on *Culex* larvae in shallow water in both island groups. Bloodworms were captured at the edge of shallow water where the flies could reach them with their "prehensile" fore legs. Occasionally, *Ochthera* were seen to alight on the water and to catch anopheline larvae in open water as well as to glide over the water and catch *Culex* larvae as they came up for air. Bohart and Gressitt (1951) observed some of these same predatory activities of *Ochthera* on Guam.

Most of the field observations on feeding in species of *Ochthera* indicate that they are nonspecific, preying on small insects of several species. In my laboratory, *O. mantis* has accepted *Drosophila melanogaster*, two chloropid species, and *Parydra quadrituberculata* as prey. Sturtevant and Wheeler (1954) listed the following species as prey of one captive species of *O. mantis tuberculata*: small dolichopodid, *Drosophila athabasca*, *Drosophila transversa*, *Drosophila putrida*, *Scaptomyza graminum*, *Leptocera* sp., *Discocerina exigua*, and *Scatella stagnalis*.

The general assumption by Dahl (1959) that the majority of adult Ephydridae are algophagous is supported to some extent by results of the few pertinent studies completed thus far. In one of these, Ping (1921) examined the gut contents of twenty larvae and ten adults of *Ephydra subopaca* and found that, in each case, they consisted almost entirely of *Chlamydomonas* (Chlorophyta) and *Navicula* diatoms (Chrysophyta). Only occasionally did he find *Mastigophora* and inorganic debris in the guts.

Brauns (1939, p. 276), in his study of the food habits of adults of *Scatella subguttata*, a halobiontic species, stated: "Die Fliege *S. subguttata* sitzt also auf dem Sandwatt und leckt jedes einzelne, vor ihr liegende Sandkorn ab. Das ablecken geschieht durch Andrucken des vorderen kahnformigen Russelteiles." The material that the flies "licked" from the sand grains was inferred to be a species of Cyanophyta, or blue-green algae. Brauns (1939, p. 277) also illustrated "die Frass-spuren von *Scatella subguttata* Meig. auf dem Farbstreifen Sandwatt . . ." (the feeding tracks or traces of the fly left on the color-streaked lower sand shore).

Tuxen (1944) studied the food habits of the thermophilic ephydrine, *Scatella thermarum* Collin, which is apparently stenotopic in and on the hot springs of Iceland. Tuxen found the food of the larvae and the adults to be identical, namely *Phormidium laminosum* Aq. and *Haplosiphon laminosus* Cohn (two species of

Cyanophyta occuring in the hot springs). Tuxen noted that the adults scraped the algae off with their labellar scrapers (prestomal teeth). He illustrated the long, convoluted gut of a larva and an adult of *S. thermarum* in substantiation of his observations on the basic phytophagy of the species.

Nemenz (1960) observed adults of *Ephydra cinerea* feeding on masses of algae (mostly *Aphanothece utahensis* Tilden and *Microcystis packardii* Farlow) washed ashore at Great Salt Lake. According to Nemenz, feeding by numerous flies left noticeable depressions in the algal mass. Brock and Brock (1968) and Brock *et al.* (1969) showed conclusively that adults and larvae of both *Ephydra bruesi* and *Paracoenia turbida* ingest, digest, and assimilate parts of bacteria and blue-green algae growing in mats on and around the effluent pools of some Yellowstone hot springs.

In the present study, a survey of the food habits of some adult Ephydridae was conducted in an attempt to determine the prevalence of algophagy in the family and especially to determine if diatoms are widely used as food. The gut

TABLE 1

A survey of the gut contents of certain adult Ephydridae.

Species examined	No. of guts dissected	Nature of gut contents	No. of diatoms per .06 mm² slide area*
Ephydrinae			
Coenia curvicauda (Meigen)	5	diatoms≅other algae	46
Ephydra niveiceps Cresson	2	mostly diatoms	125
Scatella favillacea Loew	50	mostly diatoms	76
S. obsoleta Loew	20	mostly diatoms	41
S. quadrinotata Cresson	4	mostly diatoms	90
Scatophila iowana Wheeler	4	mostly diatoms	90
Setacera atrovirens (Loew)	10	diatoms≅other algae	22
Parydrinae			
Hyadina gravida Loew	10	mostly other algae	5
Parydra appendiculata Loew	10	mostly other algae	26
P. bituberculata Loew	4	mostly diatoms	111
P. breviceps Loew	10	mostly diatoms	73
P. paullula Loew	10	mostly other algae	14
P. quadrituberculata Loew	10	mostly diatoms	105
P. tibialis Cresson	2	mostly diatoms	54
Pelina truncatula Loew	10	mostly other algae	2
Notiphilinae			
Dichaeta caudata (Fallén)	8	mostly other algae	2
Hydrellia griseola (Fallén)	10	diatom≅fungi	30
H. tibialis Cresson	15	mostly diatoms	53
Ilythea spilota (Curtis)	1	mostly diatoms	74
Notiphila macrochaeta Loew	4	mostly other algae	2
N. olivacea Cresson	5	mostly other algae	14
N. vittata Loew	5	mostly other algae	1
Oedenops nuda (Coquillett)	15	mostly diatoms	71
Paralimna punctipennis (Wied.)	6	diatoms≅other algae	27
Typopsilopa atra (Loew)	5	diatoms≅otheralgae	58
Psilopinae			
Discocerina lacteipennis Loew	10	diatoms≅other algae	32
D. orbitalis Loew	10	mostly other algae	17
D. pulchella (Meigen)	6	mostly other algae	15
Psilopa atrimana Loew	3	mostly other algae	14
P. dupla Cresson	7	mostly other algae	8

*Average number of frustules or fragments thereof for four slide areas, each 0.06 mm².

contents of representatives of 30 species in 17 genera were examined. The nature of the gut contents in all examinations was algal. At least some diatoms were found in all examinations and in those of 12 species diatoms predominated (Table 1). Additional data on the ingestion of diatoms were obtained by acidic digestion of specimens of the following species: *Scatella quadrinotata* (650 specimens), *Scatophila iowana* (1,200), *Parydra breviceps* (344), *P. quadrituberculata* (1,236), *Notiphila macrochaeta* (510), *Discocerina lacteipennis* (256), and *D. orbitalis* (105 specimens). Most of the diatoms found in *Parydra quadrituberculata* and other species occurring in the mud-shore and sand-shore habitats, as listed by Deonier (1965), were motile, pennate benthic forms, usually occurring on the surface of bottom silt in shallow water or on newly exposed shoreline. The most common genera represented were *Navicula*, *Pinnularia*, *Nitzschia*, *Gyrosigma*, *Hantzschia*, and *Surirella*.

A sizable proportion of the diatoms in most of the gut examinations were fragmented, so the possibility of accessorial ingestion of fragmented diatom frustules exists. However, examination of the crops of four specimens of *Scatella obsoleta* showed mostly unbroken diatom frustules, whereas the gut posterior to the crop contained only a few unbroken frustules. This observation may indicate that the frustules are broken during passage through the gut, perhaps as a result of packing and gut-wall contraction.

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